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Correlation of morphological variations in the seedling of Phaseolus vulgaris

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INTRODUCTORY REMARKS

During the past several years one of us has had under way extensive experiments on the differential death-rate of bean seedlings. Individuals differing in structure also differ in their capacity for survival under field conditions,* and in such physiological characteristics as capacity for the development of the tissues of the primordial† and of the subsequent leaves.‡

Some tens of thousands of seedlings of known morphological characteristics have been exposed to risk, as the life insurance statisticians express it, in an attempt to determine the selective value of the various morphological variations. These seedlings were, for technical reasons, necessarily planted in the field at a time when the cotyledonary node and the primordial node only could be studied. It is evident that the capacity of the plant for survival may be in some degree dependent upon characters developed later in ontogenesis, but correlated with characters of the first or second node of the seedling.

However this may be, it is certainly true that a full knowledge of the morphology and physiology of the variant bean seedling demands a thoroughgoing investigation of the correlation between the structure of the first two leaf whorls and that of later whorls. We have, therefore, been forced to consider the problem of the morphological character of the leaf whorls produced at the third node in the case of plants showing various structural abnormalities at the first two nodes.

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* Harris, J. Arthur. A simple demonstration of the action of natural selection. Science II. 36: 713–715. 1912.

† Harris, J. Arthur. Studies on the correlation of morphological and physiological characters: the development of the primordial leaves in teratological bean seedlings. Genetics 1: 185–196. 1916.

‡ Harris, J. Arthur. Further studies on the interrelationship of morphological and physiological characters in seedlings of *Phaseolus*. Mem. Brooklyn Bot. Gard. 1. *In press.*

Phaseolus is well suited for such investigations. The normal seedling has two cotyledons, inserted at the same level, and two opposite primordial leaves. A large number of structural variations, four types of which will be considered in this paper, may occur. The chief disadvantage lies in the rarity of many of the variations in the lines with which we have dealt. The securing of adequate series is excessively laborious. The present paper is based upon a careful study of the variations in the first three nodes of 16,348 plants, which were selected from about 450,000 seedlings examined for the characters of the first and second node.

When in the following paragraphs we refer to normal and abnormal plants or seedlings, it must be understood that this applies to the characteristics of the individual as determined on the basis of the first two nodes, the cotyledonary and the primordial only. In its later development the "abnormal" plant may remain "abnormal" or become "normal," and the "normal" plant may either continue to be "normal" or become "abnormal."

The nature and method of classification of the abnormalities dealt with will be discussed in the presentation of the data below.

MATERIALS AND METHODS

The materials upon which this study is based are a series of lines of White Navy beans grown at the Station for Experimental Evolution during the past several years. The seeds were harvested from field cultures in 1915 and germinated in sand in the autumn of 1916.

Seedlings which were abnormal in the characters of the first or second node, i. e., in the number or insertion of the cotyledons or of the primordial leaves, were sorted out for potting in soil and subsequent study of the third node, that normally giving rise to the first compound leaf.

For each abnormal individual, a normal control seedling from the same parent plant was taken at random to serve as a basis of comparison. Both were potted in soil and grown to a stage when the characteristics of the third node could be accurately determined.

For the onerous preliminary examination of nearly a half a million seedlings we are greatly indebted to Miss Edna K. Lockwood, Miss Margaret Gavin and especially to Miss Lillie Gavin.

PRESENTATION AND ANALYSIS OF DATA

The slightest abnormality which we have been able to discover occurring in considerable numbers of bean seedlings is the vertical separation of the two normally opposite cotyledons. So imperceptible is the line of transition between normal and abnormal that personal equation must play some part in classification. The cotyledons may be much more widely separated. The variation is a purely graduated one, with no sharp lines of demarcation between the different degrees of separation. Generally we have recognized three grades, but because of the rarity of plants with more widely separated cotyledons we have in this paper grouped our data into two classes only. The first comprises plants with cotyledons 2–3 mm. apart. The second includes all those in which they are more distant.

The number as well as the position of the cotyledons may vary. Plants with three instead of two cotyledons fall into two groups; those with the normal pair of primordial leaves and those with a whorl of three leaves. The latter are by far the more abundant.

Abnormality developed subsequently to the selection of the seedlings in the preliminary sorting may affect either the internode between the second and the third nodes, that is, between the primordial leaf whorl and the point of insertion of the first compound leaf or leaf whorl, or it may be confined to the number or structure (or number and structure) of the leaves inserted at the third node.

In the original selection of individuals abnormal in the characters of the first or second node, only those with sensibly normal axes (hypocotyl and epicotyl) were chosen for the purposes of the present study.

Two types of abnormality in the axis beyond the second (the primordial) node have been considered.

The first is a sensible broadening of the axis, identical with or similar to fasciation. This is a graduated character. The line of demarcation between normal and abnormal is not clearly marked.

and personal equation may influence in some degree the classification of the seedlings.

The second is a division of the axis into two coördinate branches each with a terminal bud.

The frequencies of the two types of axial variation are too small to justify detailed discussion. The entries in TABLE I show that

TABLE I

FREQUENCIES OF ABNORMALITY OF SECOND INTERNODE IN NORMAL AND ABNORMAL SEEDLINGS

Class of abnormality	Actual frequencies			Percentage frequencies		
	Normal internode	Broadened internode	Divided internode	Normal internode	Broadened internode	Divided internode
Two cotyledons slightly separated; two primordial leaves	4,017	5	8	99.6774	.1240	.1985
Normal control	4,029	0	1	99.9751	......	.0248
Difference	−12	+ 5	+ 7	−.2977	+ .1240	+.1737
Two cotyledons widely separated; two primordial leaves	878	2	1	99.6594	.2270	.1135
Normal control	881	0	0	100.0000	......	......
Difference	−3	+ 2	+ 1	−.3406	+ .2270	+.1135
Three cotyledons; two primordial leaves	813	12	0	98.5454	1.4546	......
Normal control	825	0	0	100.0000	......	......
Difference	−12	+12	0	−1.4546	+1.4546	......
Three cotyledons; three primordial leaves	2,410	14	14	98.8515	.5742	.5742
Normal control	2,436	2	0	99.9179	.0820	......
Difference	−26	+12	+14	−1.0664	+ .4922	+.5742

in every instance in which any individuals at all are available the seedlings which are abnormal in either the cotyledonary or the primordial node show a higher percentage of abnormality in the structure of the internode beyond the second node than do the normal controls.

We now turn to a consideration of variation in the leaves inserted at the third node. The leaves of plants with abnormality of the axis should not be combined with those having normal axes. They are not sufficiently numerous for separate consideration.

Confining our attention to seedlings which have a normal axis for at least the length of the second internode of the epicotyl, we have the frequencies shown in TABLES II–V.* The character of the control plants is also given.

TABLE II

SEEDLINGS WITH TWO COTYLEDONS SLIGHTLY SEPARATED AND TWO PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	3,791	3,853	94.37	95.63	−1.26
2	225	176	5.60	4.37	+1.23
3	1	0	.02	.00	+ .02
Totals......	4,017	4,029	99.99	100.00	

TABLE III

SEEDLINGS WITH TWO COTYLEDONS WIDELY SEPARATED AND TWO PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	811	840	92.37	95.35	−2.98
2	67	41	7.63	4.65	+2.98
Totals......	878	881	100.00	100.00	

TABLE IV

SEEDLINGS WITH THREE COTYLEDONS AND TWO PRIMORDIAL LEAVES

Numbes of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	591	792	72.69	96.00	−23.31
2	221	33	27.18	4.00	+23.18
3	1	0	.12	.00	+ .12
Totals......	813	825	99.99	100.00	

TABLE V

SEEDLINGS WITH THREE COTYLEDONS AND THREE PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	1,632	2,200	67.72	90.31	−22.59
2	771	236	31.99	9.69	+22.30
3	7	0	.29	.00	+ .29
Totals......	2,410	2,436	100.00	100.00	......

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* In these tables the numbers of control plants are not exactly identical with the numbers of abnormal plants, since some of those selected as normal in the seedling stage showed abnormality of the axis in subsequent development and are omitted here, where we are discussing abnormalities of foliar characters only.

In each of the types of abnormality dealt with the abnormal series show a higher proportion of the individuals with two or three leaves at the third node than do their normal controls.

Furthermore, seedlings showing different types of abnormality at the first nodes also differ among themselves in the extent of abnormality at the third node. Thus plants which are normal except for slight separation of the cotyledons have two or three leaves at the second node instead of the single leaf normally found in 5.63 per cent. of the individuals. Plants with the cotyledons more widely separated have 7.63 per cent. of their number with two or three instead of a single leaf.

When one turns to the groups of plants which have three instead of two cotyledons, a conspicuous difference is at once apparent. Plants which have three cotyledons and a normal pair of primordial leaves produce two or three instead of a single leaf at the third node in 27.31 per cent. of the cases. Seedlings with three cotyledons and a whorl of three primordial leaves instead of the normal pair at the third node have 32.29 per cent. of the individuals with two or three leaves at the third node.

Heretofore the number of leaves inserted at the third node has furnished the only measure of variation at this region of the axis. We now propose to consider variation in the organization of the leaves themselves. It will not be possible to do this in the detail in which we hope to treat the problem ultimately. The range of variation in the division of the bean leaf is rather great, and the laws governing it are doubtless very complicated. Some progress has already been made on the problem, but for the present we shall limit our discussion to the number of leaflets, leaving the problem of their arrangement for treatment when even larger series of data are at our disposal.

The actual frequencies of number of leaflets per leaf produced at the third node are shown in TABLE VI.

The most conspicuous feature of this table is the bimodal nature of the distribution. The modes are on three and six, as is to be expected from the fact that the distribution of the whole number of leaflets depends upon plants with from one to three leaves at the third node.

Because of the wide range of variation in leaflet number it is not feasible to reduce these frequencies for the individual classes to a percentage basis for comparisons. This has, however, been done for larger groups secured by combining all the seedlings showing merely separation of the cotyledons and all those showing three cotyledons instead of the normal two. The results are shown in the accompanying TABLE VII, which is self explanatory.

TABLE VI

NUMBER OF LEAFLETS PRODUCED AT THE THIRD NODE BY SEEDLINGS OF VARIOUS TYPES

Number of leaflets	Two cotyledons slightly separated and two primordial leaves		Two cotyledons widely separated and two primordial leaves		Three cotyledons and two primordial leaves		Three cotyledons and three primordial leaves	
	Abnormal	Control	Abnormal	Control	Abnormal	Control	Abnormal	Control
1	5	2	1	...	1	...	....	....
2	16	6	4	...	3	2	2	5
3	3,741	3,825	801	835	572	782	1,602	2,185
4	27	21	5	4	14	5	28	8
5	10	2	1	2	6	3	9	2
6	215	173	65	40	203	33	751	236
7	1	....	1	...	12	...	12	....
8	....	....	...	...	1	...	....	....
9	1	....	...	...	1	...	3	....
10	1	....	...	...	...	...	2	....
11	....	....	...	...	...	...	1	....
Totals	4,017	4,029	878	881	813	825	2,410	2,436

TABLE VII

COMPARISON OF THE NUMBER OF LEAFLETS IN DICOTYLEDONOUS AND TRICOTYLEDONOUS SEEDLINGS WITH THAT IN THEIR NORMAL CONTROLS

Number of leaflets	Seedlings with cotyledons separated		Seedlings with three cotyledons	
	Abnormal	Control	Abnormal	Control
1	.12	.04	.03	....
2	.41	.12	.16	.21
3	92.79	94.91	67.45	90.98
4	.65	.51	1.30	.40
5	.22	.08	.47	.15
6	5.72	3.52	29.60	8.25
7	.04	.81	.74	....
8	....	....	.03	....
9	.02	....	.12	....
10	.02	....	.06	....
11	....	....	.03	....

A comparison may be made without the combination of different grades of abnormality by grouping the number of leaflets around the modal classes 3, 6 and 9. The results in TABLE VIII show essentially the same relationships as those given in TABLES VI–VII. First, the higher leaflet numbers are more extensively represented in the abnormal plants of each of the four types than they are in the controls. Second, the tricotyledonous plants show a far greater increase in the number of leaflets inserted at the third node than do those abnormal only in the position at which the two cotyledons are inserted.

TABLE VIII

PERCENTAGE FREQUENCIES OF NUMBERS OF LEAFLETS IN SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Number of leaflets		
	1–4	5–7	8–11
Two cotyledons slightly separated and two primordial leaves	94.32	5.62	.05
Control	95.66	4.34	....
Difference	− 1.34	+ 1.28	+.05
Two cotyledons widely separated and two primordial leaves	92.37	7.63	....
Control	95.23	4.77	....
Difference	− 2.86	+ 2.86	....
Three cotyledons and two primordial leaves	72.57	27.18	.24
Control	95.64	4.36	....
Difference	−23.07	+22.82	+.24
Three cotyledons and three primordial leaves	67.72	32.03	.25
Control	90.23	9.77	....
Difference	−22.51	+22.26	+.25

In substantiation of these conclusions the reader will note that in the class with slightly separated cotyledons 5.68 per cent. of the plants have from five to ten leaflets as compared with 4.34 per cent. with five and six leaflets in the control series. In seedlings with more widely separated cotyledons but no other abnormality there are 7.63 per cent. of the plants with five to seven leaflets as compared with 4.77 per cent. of the normal controls with five or six leaflets. Seedlings with three cotyledons but the normal number of primordial leaves have 27.43 per cent. of the individuals with from five to nine leaflets as compared with 4.36 per cent. with five or six leaflets in the normal controls.

Plants with a trimerous cotyledonary and primordial whorl have 32.28 per cent. of the seedlings with from five to eleven leaflets as compared with 9.77 per cent. with five and six leaflets in the normal controls.

Taking the average number of leaflets per plant as a basis of comparison between the abnormal plants and their controls we find the results in TABLE IX.

TABLE IX

MEAN NUMBER OF LEAFLETS IN SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Mean number of leaflets in abnormals	Mean number of leaflets in controls	Difference
Two cotyledons slightly separated; two primordial leaves	3.170	3.133	+0.037
Two cotyledons widely separated; two primordial leaves	3.228	3.191	+0.037
Three cotyledons; two primordial leaves	3.847	3.131	+0.716
Three cotyledons; three primordial leaves	3.990	3.294	+0.606

Note (*a*) that for each type of normality the average number of leaflets is greater in the abnormal individuals than in the normal, and (*b*) that the difference between the abnormal class and its control is far greater in the case of the plants with three cotyledons than in those in which the abnormality in the cotyledonary whorl consists merely in the separation of the two cotyledons.

Thus the results for number of leaflets substantiates the conclusion based upon number of leaves.

Evidently, however, the number of leaflets is to a great extent determined by the number of leaves. The problem now arises: Are there differences in the average number of leaflets per leaf in the abnormal and normal individuals?

Means and their differences have been determined, but are so slight that conclusions must be deferred until further series of data are available.

Just one other method of dealing with the problem of the correlation in structural variation may now be considered.

Number of leaflets is, in the materials dealt with, practically an integral variate. In examining a large series of plants those with partial division of a leaflet, representing transition stages between a leaf with n and one with $n + 1$ leaflets are sometimes found. Such cases are, however, relatively rare. The lobing of the leaflet has therefore been disregarded in the foregoing treatment. A leaf with three leaflets, one of which has a lobe, has been recorded as 3 in the tables, not as an intermediate between three and four. This has simplified the tabling of the data, and the calculation of the simple constants necessary to the interpretation the data, without any material loss in accuracy.

One may, however, inquire whether there are differences in the degree of lobing of the leaflets produced at the third node in plants which are normal and in plants which are abnormal in the characters of the first and second node. Because of the very low percentages of lobing in the leaflet no stress whatever is to be laid upon the exact values found, even in samples containing several hundreds or thousands of plants, because of the great difficulties of determining the probable error of a small percentage.

The results are given in TABLE X.

TABLE X

PERCENTAGE OF LOBING IN THE LEAVES OF SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Abnormal plants	Control plants	Difference
Two cotyledons slightly separated; two primordial leaves	0.349	0.273	+0.076
Two cotyledons widely separated; two primordial leaves	0.456	0.112	+0.344
Three cotyledons; two primordial leaves	1.599	0.242	+1.357
Three cotyledons; three primordial leaves	0.954	0.328	+0.626

Here the percentage frequency of plants with one or two lobes on the leaflets* are given for each type of abnormality dealt with and compared with that found in the control series.

Two relationships seem clearly indicated by the constants in this table.

First, the tendency to the production of lobes is greater in the leaflets produced by abnormal plants of all four types than in their normal controls.

Second, the tendency to the production of lobes is greater in the leaflets of plants with a trimerous cotyledonary whorl, and either a dimerous or trimerous primordial whorl, than it is in plants in which the sole abnormality consists in the separation of the two cotyledons in their insertion on the axis of the plant.

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* In the case of two lobes both may occur on the same leaflet or they may be on different leaflets.

RECAPITULATION

This paper presents the results of a first attempt to determine some of the correlations in the structural variations of the seedling of *Phaseolus vulgaris*.

The materials are drawn from a series of lines of Navy beans grown for the past several years at the Station for Experimental Evolution. The seeds used were harvested from plants of selected ancestry. Neither of these factors will, we believe, invalidate the conclusions drawn in this paper. These conclusions will not necessarily apply to certain entirely abnormal races.

Fasciation-like broadening of the axis and longitudinal division of the axis distal to the insertion of the primordial leaves are both more frequent in seedlings showing separation of the cotyledons and in tricotyledonous seedlings than in those which are normal.

Seedlings which are normal except for the separation of the cotyledons and those which have three cotyledons and a normal pair of primordial leaves or three cotyledons and a whorl of three primordial leaves produce a larger number of leaves, a larger number of leaflets and a higher percentage of leaves with lobes at the third node than do those which are normal in their cotyledonary and primordial leaf characters.

Seedlings which are tricotyledonous, with either a normal pair or a whorl of three primordial leaves, show higher percentages of variation in the axis, or the leaves produced by the axis, distal to the primordial leaves than do those which are normal except for the separation of the two cotyledons.

These studies will be continued.

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